

would indicate a probable origin in central Arizona, radiating into all western states except perhaps, Washington and Montana.

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CHROMOSOME NUMBERS AND A PROPOSAL FOR CLASSIFICATION IN SISYRINCHIUM (IRIDACEAE)

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INTRODUCTION

The classification of North American *Sisyrinchium* has been highly unsatisfactory for many decades. For example, it is difficult with the aid of standard floras such as Abrams (1923), Fernald (1950), Gleason (1952), and Munz (1959) to identify many collections of this genus from regions covered by these floras. One reason for this difficulty is that plants of this genus are notoriously lacking in qualitative differences such as are necessary to distinguish species. A second reason is that regional floras which deal with different or confluent parts of the continent have continued to follow traditional and local classifications. The existing disagreements concerning the occurrence and the nature of phenotypic discontinuities illustrates the need for a reappraisal of variability not only by the use of techniques of modern taxonomy but by examination of variation on a continent-wide basis. The present paper brings together some field, herbarium, published, and laboratory observations on correlations between morphology, chromosome numbers, ecology, and geography of plants of this genus from populations throughout much of the North American distribution area.

The *Sisyrinchium* populations considered in this paper comprise the widely distributed, small-flowered perennials in which the anther filaments are united in a tube. Excluded are the annuals of Texas and adjacent regions which have been discussed recently by Shinners (1962). Also excluded are the large-flowered perennials of Mexico and the Caribbean Islands as well as the large-flowered and very distinctive *S. douglasii* Dietr. of western North America. So defined, the plants commented on in this paper range from Greenland to Alaska and south to Florida, Texas, and California and may extend into Mexico.

Directly relevant to their classification and an outstanding feature of the *Sisyrinchium* populations considered here is that a high degree of self-pollination appears to be a characteristic feature (Knuth, 1909; Ingram, 1967; Table 1). Table 1 shows the results of an experiment designed to determine the potential for automatic self-pollination in a tetraploid population growing under natural conditions near Banff,

TABLE 1. SEED SET RESULTING FROM ARTIFICIAL BAGGING EXPERIMENTS
IN WILD PLANTS OF *SISYRINCHIUM BERMUDIANA*

Data from a 12-ploid population about 6 miles west of Banff, Alberta, Canada (vouchers *Mosquin & Seaborn 7048* and *7164*, DAO).

Number of individual plant	Number of capsules on inflorescence	Number of seeds per capsule	Number of seeds in control capsules (adjacent plants)
7048-1	3	3 ; 26 ; 8	16
7048-2	2	3 ; 16	33
7048-3	2	6 ; 6	20
7048-4	1	32	30
7048-5	3	3 ; 5 ; 25	24
7048-6	1	1	28

Alberta. The pollination bags used in this experiment were white and highly porous. They were made from synthetic material especially designed for tree-breeding work in the field and do not deteriorate under usual field conditions. The plants were bagged on June 25 and the data collected on July 29, 1968. The bagged plants of this population, isolated from insects, produced nearly 45% seed set as compared with the controls. There can be no doubt, therefore, not only that these plants were self-compatible but that they are highly homozygous. A consideration of the morphological effects of self-pollination (Stebbins, 1957) reads like a description of the variation pattern of wild populations considered here. Thus local populations are highly uniform morphologically, while conspicuous differences often occur between geographically isolated colonies. Intermediates are common between character extremes. Morphologically very similar plants occur in widely separated places, for example on the American northwest coast and in the Appalachian region, and again in Greenland and the western United States.

Another feature of the *Sisyrrinchium* populations considered here is polyploidy, an important evolutionary mechanism. To date the numbers $2n = 16, 32, 64, 82, 84, 88, 90,$ and 96 have been reported among these plants (Bowden, 1945; Löve and Löve, 1958; 1961; Lewis and Oliver, 1961; Oliver and Lewis, 1962; Clapman, et al.; 1962; Böcher, 1966; Oliver, 1966; Ingram, 1967; table 2). It is possible, therefore, that in some places chromosome numbers might provide the necessary key for discovering corresponding morphological breaks.

In closely related species, differences in chromosome numbers are frequently reflected in differences in pollen grain size. This is, however, not so in *Sisyrrinchium*, where I have found that tetraploids may have pollen as large as the 12-ploids. It is of interest that Böcher (1966) in

TABLE 2. CHROMOSOME NUMBERS.

Sisyrinchium arenicola Bicknell. $2n = 32$: NORTH CAROLINA, Moore Co., 2.7 mi S of Pine Bluff, *Mosquin & Mosquin 5935* (COLO, DAO).

S. bellum Wats. $n = 16$: CALIFORNIA, San Diego Co., Santa Ysabel, *Mosquin & Snow 3974* (COLO., DAO); several mi W of San Pasqual, *Mosquin & Snow 3975* (COLO, DAO). $2n = ca\ 90$ CALIFORNIA, Inyo Co., 6.7 mi W of the Lee Vining Junction along Tioga Pass Hwy, *Mosquin 4780* (COLO, DAO, DS, UAC).

S. bermudiana L. $2n = 32$: ALBERTA, about 6 miles west of Banff, *Mosquin & Seaborn 7164*. CALIFORNIA, Plumas Co., about 2 mi SE of Graegle, *Mosquin & Gillett 5305* (COLO, DAO). $n = 16$: NEVADA, Lyon Co., road to Virginia City near Hwy 50, *Gillett & Moulds 12700* (COLO, DAO). $2n = ca\ 64$: MONTANA, Meagher Co., Ringling, *Mosquin & Gillett 5226* (DAO); Missoula Co., 13.9 mi W of Lolo, *Mosquin & Gillett 5262* (DAO). TEXAS, Van Zandt Co., 12.7 mi E of Terrell, *Mosquin & Mosquin 5469* (DAO, DS); Galveston Co., Galveston Island, near SW tip of the Island, about 22 mi SW of Galveston, *Mosquin & Mosquin 5529* (DAO). $2n = 96$: ALBERTA, 7.5 mi S of the Trans Canada Hwy, along road to Kananaskis Lakes, *Mosquin & Benn 5185* (COLO, DAO, UAC). BRITISH COLUMBIA, 7.7 mi E of Galloway (no voucher). CALIFORNIA, Sierra Co., along road from State Hwy 89 to Independence Lake (DAO). MONTANA, Cascade Co., 15 mi E of Great Falls, *Mosquin & Gillett 5215* (DAO); Jefferson Co., 1.5 mi E of Pipestone Pass, *Mosquin & Gillett 5261* (COLO, DAO, UAC). NEW BRUNSWICK, Restigouche Co., 20 mi NE of Kedgwick, *Mosquin & Spicer 6374* (DAO). ONTARIO, Norfolk Co., Turkey Point, *Bowden 138-55* (DAO); Carleton Co., 3 mi SW of North Gower, *Mosquin & Frankton 6519* (DAO). QUEBEC, Bonaventure Co., 1 mi W of Nouvelle, *Mosquin & Spicer 6366* (DAO); Gaspé Co., at lodge about 2 mi N of Mt. Albert, *Mosquin & Spicer 5997* (DAO); 9 mi W of Petite Vallée, *Mosquin & Spicer 6346* (COLO, DAO); Rimouski Co., about 6 mi SW of Ste. Flavie, *Mosquin & Spicer 5997* (COLO, DAO); Stanstead Co., about 5 mi due E of Fitch Bay, *Mosquin & Spicer 6338* (DAO). SOUTH DAKOTA, Pennington Co., 1.9 mi NE of Hill City, *Mosquin & Mulligan 5148* (COLO, DAO).

comparing tetraploids and 12-ploids found that seed diameter in the former was 0.7-0.8 mm, while in the latter it ranged from 1.1 to 1.4 mm, but the sample size was small. Seed diameter in the 12-ploid plants from Banff referred to in Table 1 ranged from 0.7 to 1.1 mm.

Yet another feature of the genus considered here, and one that has contributed to the creation of many names of dubious value, is the wide ecological diversity of the wild populations. This diversity is evident from the habitat descriptions in various floras and from first-hand field observations. Wild populations occur in montane meadows, sage deserts, prairies, and seashores, and often along roads as weeds.

TAXONOMY

Among the many species names currently in use for the American populations of *Sisyrinchium*, the most widely employed are perhaps *S. angustifolium* Mill. and *S. montanum* Greene. The former is applied to eastern North American populations from eastern Canada to Florida and Texas (Fernald, 1950; Shinnery, 1963); the latter most often to western populations from the Northwest Territories and British Colum-

bia south to Colorado, but also eastward to New York, eastern Canada, and Greenland (Fernald, 1950; Böcher, 1966). The most important character by which these two species are purported to differ is branching, *S. angustifolium* being branched and *S. montanum* unbranched. It is very common, however, to find both branched and unbranched plants in many populations, although one type is usually much more frequent than the other. It would be much more useful, therefore, to consider these two species to be conspecific, as Rydberg (1932) thought. Another widely used name is *S. idahoense* Bicknell. Yet plants of this species from Idaho, Oregon, and California do not differ in any single trait or combination of traits from the *S. montanum*—*S. angustifolium* populations considered above. Similarly some other names which are currently used in floras appear to apply to populations which have morphological traits well within the range of variability of the populations considered above. Thus species like *S. campestre* Bicknell, *S. albidum* Raf., *S. graminoides* Bicknell (see Shinnars, 1962, for discussion of this name), *S. langloisii* Greene, *S. sagittiferum* Bicknell, *S. littorale* Greene, *S. sarmentosum* Suksdorf, and *S. halophilum* Greene, as far as I can judge from descriptions in floras and also from comparisons of herbarium specimens, are very likely best treated within a single widespread species. The correct name for this widespread species appears to be *S. bermudiana* L. (Shinnars, 1962).

Several additional species have been described which, in contrast to those mentioned above, are, at least in their morphological characteristics, modally distinct from *S. bermudiana*. These are *S. atlanticum* Bicknell, *S. mucronatum* Greene, *S. arenicola* Bicknell, *S. capillare* Bicknell, and in the west perhaps *S. bellum* Wats., although many populations of the last species, particularly from the Sierra Nevada of California, would readily pass for collections from the eastern United States (see Munz, 1959, for brief discussion of *S. bellum*.)

CORRELATIONS AND DISCUSSION

Correlations between morphological characters on the one hand and ecology, chromosome number, distribution, and breeding habit on the other provide the basis for contemplating the details of a classification that not only would be readily usable but would closely reflect our present knowledge of genetic relationship. Perhaps the most important correlation between these characteristics in *Sisyrinchium*, and one that is of vital significance to the classification of this genus, is a negative one, namely, morphological differentiation is, for the most part, not associated with chromosomal differentiation. Hence chromosome numbers will not play an important role in helping to construct a useful classification for this genus.

Another fact is that ecological similarities or differences very frequently are not accompanied by corresponding morphological patterns. For example, a population from a marshy habitat in sage desert near

Virginia City, Nevada (*Gillett & Moulds 12700*, DAO), is virtually identical in all features of external morphology with plants collected on dry grassy stream banks in montane yellow pine forest of the Sierra Nevada (*Mosquin & Gillett 5307*, DAO). In this example the former colony is tetraploid while the latter is 12-ploid. In yet another case, the octoploid populations of Montana do not appear to differ ecologically from the geographically adjacent 12-ploid colonies. Neither do these two chromosome races in Montana differ morphologically in any perceivable way. As a last example, plants of Greenland (*Böcher, 1966*) are essentially identical with many populations in the western United States; the Greenland plants are tetraploid, while at least three chromosome races (tetraploid, octoploid, and 12-ploid) are found in the western United States. Other examples could be cited. That such relationships may also occur in other species of *Sisyrrinchium* is suggested from reports of the numbers $n = 8, 16,$ and 48 and $2n = 96$ from *S. atlanticum* Bicknell (*Löve and Löve, 1958; Oliver and Lewis, 1962; Oliver, 1966*).

The geographical distribution of the chromosome races of *S. bermudiana* is of interest. The tetraploids occur in southern portions of the United States, in the Great Plains, in western Alberta, in California, and, surprisingly, in Greenland. Octoploids are known only from Texas and Montana, while 12-ploid populations are very widespread in the northern regions and also occur in the Queen Charlotte Islands, British Columbia (*Taylor and Mulligan, 1968*). Figure 1 gives the distribution of the chromosome races. Evolution by aneuploid decrease from $2n = 96$ is clearly occurring in the eastern United States, with numbers as low as $2n = 82$ recorded (*Ingram, 1967*). The count of $2n = 90$ (*Bowden, 1945; and present paper*) from the Sierra Nevada suggests that an aneuploid reduction series from $2n = 96$ may also be present in the western United States.

The geographical origin of the Greenland tetraploids poses a special problem. It would be useful to determine the chromosome number of populations in Newfoundland and particularly in the vicinity of Goose Bay, Labrador, since presumably the Greenland tetraploids originated from some locality in northeastern North America.

Some additional reports of chromosome numbers in *S. bermudiana* have been published by *Löve and Löve (1958)* under different species names. These are given in their paper as having been determined from "many plants from the southern and eastern parts of the province of Quebec" and from "northern Virginia" ($2n = 96$ as *S. angustifolium*), from "the Canadian prairies" and from "a few places in Ontario and Quebec" ($2n = 32$ as *S. montanum*), and from "a couple of localities in southern Wisconsin and Ontario" ($2n = 32$ as *S. albidum*). These report could not be included in Fig. 1 because the exact localities and voucher information were not given in the paper. *Löve and Löve* also report having determined the number $2n = 96$ from plants of

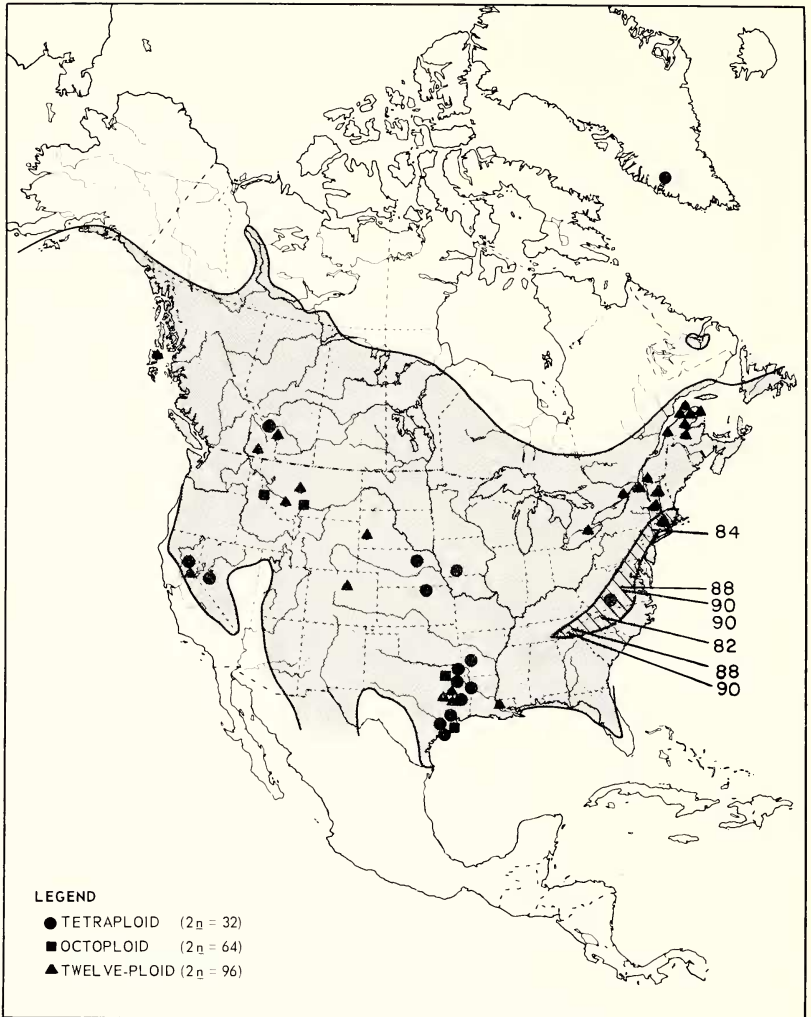


FIG. 1. Distribution of *Sisyrinchium bermudiana* (dotted area) showing locations of populations with chromosome counts. Chromosome counts previously reported under the names *S. albidum* (Bowden, 1945; Oliver and Lewis, 1962), *S. angustifolium* (Bowden, 1945), *S. campestre* (Oliver and Lewis, 1962; Oliver, 1966), *S. groenlandicum* (Böcher, 1966), *S. langloisii* (Oliver and Lewis, 1962), and *S. montanum* (Ingram, 1967) are included. The counts for *S. bermudiana* given by Ingram (1967) are also included.

S. bermudiana from "several localities in Britain and Scandinavia," as well as the number $2n = 64$ from one Irish population which they describe as a new species (Löve and Löve, 1961). The correct number of the Irish population has now been shown to be $2n = 88$ (Ingram, 1967). The morphology and chromosome number of the Irish plants fall well

into the range of variability of *S. bermudiana* even when grown under similar conditions in the greenhouse (Ingram, 1967). In a detailed study of the Ireland plants Ingram concluded that they should be most usefully treated as *S. bermudiana*. There seems little doubt that adopting a wide species concept for the North American *Sisyrrinchiums* would provide biologists with a maximally useful classification.

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